



TERRITORIALITY AND BREEDING STATUS OF COYOTES RELATIVE TO SHEEP PREDATION

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Abstract: Coyote (*Canis latrans*) depredation is a chronic problem for sheep producers in the western United States. Due to increasingly localized control efforts, behavior of individual coyotes in sheep-ranching environments is becoming a more important consideration. We radiotracked 14 coyotes on a year-round sheep-ranching facility in north-coastal California during September 1993–December 1995. Breeding coyote pairs used mutually exclusive territories (maximum overlap between 90% adaptive kernel home ranges = 4%). Nonbreeding coyotes were transient or varied in their degree of fidelity to putative natal territories but generally avoided cores of nonnatal territories. Breeding coyotes whose territories contained sheep were the principal predators of sheep. In the 1994 lambing period (1 Jan–31 May), radiotelemetry indicated that 1 breeding male was responsible for 71% of 65 kills. In the 1995 lambing period, 4 breeding pairs were strongly implicated in 92% of 48 kills and were suspected of 85% of 26 additional kills; nonbreeders were not associated with sheep depredation. Depredation was reduced only when territorial breeders known to kill sheep were removed. These results suggest the need for management to target breeding adults in the immediate vicinity of depredation. Efforts to remove individuals >1 territory-width away from problem sites are unlikely to reduce depredation and may exacerbate the problem by creating vacancies for new breeders that might kill sheep.

JOURNAL OF WILDLIFE MANAGEMENT 63(2):593–605

Key words: breeding status, California, *Canis latrans*, coyote, predation, sheep, space use, territoriality.

Coyote depredation is a chronic problem for livestock producers in the western United States and is viewed as a major cause of the decline of the sheep industry (Wagner 1988).

Although coarse-scale studies have examined population dynamics of coyotes in sheep-producing regions (Knowlton 1972, Connolly and Longhurst 1975), most behavioral research on coyotes has been conducted in areas without sheep. Consequently, little information exists on coyote behavior in the presence of sheep. This finer-scale information is increasingly important due to a change, in recent years, of the spatial

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scale over which depredation problems occur. As the number of sheep operations has dwindled, those remaining have become more isolated. This trend, combined with restrictions on toxicant use, has changed the scale of coyote management, with regional population reduction giving way to local control on individual ranches or grazing allotments.

We investigated territoriality and sheep-killing behavior of coyotes on a large, year-round sheep ranch. Previous studies have examined coyote space use and social behavior in areas where there are no sheep (Camenzind 1978, Bekoff and Wells 1980; Bowen 1981, 1982). A few studies have addressed coyote space use and behavior in environments where sheep or goats were seasonally grazed (Mills and Knowlton 1991, Shivik et al. 1996) or experimentally introduced (Windberg et al. 1997), but we are unaware of any study of free-ranging coyotes on a year-round sheep ranch.

We did not expect all coyotes in an area to have equal access to pastured sheep, due to coyote social dynamics and space-use patterns. Coyotes are territorial (Camenzind 1978, Bowen 1982, Messier and Barrette 1982), which implies relatively exclusive use of food and other resources within the territory by the resident pair or pack (i.e., including nonbreeding associates). However, the presence of sheep may affect social and spatial characteristics of coyotes. During a food shortage in Wyoming, large aggregations of transient coyotes sometimes formed at elk (*Cervus elaphus*) carcasses (an important winter food source), overwhelming the ability of territorial coyotes to defend them (Camenzind 1978). Because of the seemingly defenseless nature of sheep (especially lambs) and their local abundance on year-round sheep ranches, coyotes might be expected to gravitate toward sheep with a similar effect (Young and Jackson 1951:225; Shivik et al. 1996). Further, resident coyotes might be less able to defend territories with sheep because dispersed resources are generally more difficult to defend than clumped resources (Bekoff and Wells 1980). Alternatively, coyotes might not be attracted to sheep where wild prey are abundant, such that territoriality and foraging habits are unaffected by the presence of sheep.

We also identified a need to determine which individuals kill sheep. Within packs, foraging behavior and diet may differ by social rank, with dominant, breeding animals killing most wild

ungulates (Bowen 1981, Gese and Grothe 1995) and subordinate individuals more often killing small prey (Gese et al. 1996a). Although available evidence suggests not all coyotes are equally likely to kill sheep (Gier 1968, Conner et al. 1998), characteristics of coyotes associated with sheep-killing behavior are poorly understood. We sought to understand the depredation problem from a behavioral and ecological perspective in a typical ranching environment, where coyote mortality from humans was high and sheep represented an abundant resource. Our objectives were to determine the degree of exclusivity of coyote territories and to characterize sheep-killing coyotes in terms of breeding status, sex, and space use.

STUDY AREA

The Hopland Research and Extension Center (HREC) is a University of California agricultural research station located in the mountains of the North Coast Range, Mendocino County, California. The facility encompasses 2,168 ha that range from 150 to 900 m in elevation. The topography is hilly to rugged, with a primarily southwest aspect. The climate is characterized by hot, dry summers and mild, wet winters. Average annual precipitation is about 100 cm and falls mostly as rain between November and February. Major vegetation types were annual grassland, chaparral, oak woodland, and mixed evergreen-deciduous forest. The vegetation of HREC was described in detail by Murphy and Heady (1983).

The HREC has been used for research on sheep production since 1951. Flocks of 900–1,500 adult ewes are rotated among 32 fenced pastures. The addition of lambs roughly doubles the existing sheep population between December and May, with peak numbers of lambs pastured from mid-January to mid-March. Coyote predation of sheep on HREC has been considered a problem since the early 1970s.

The HREC is similar to other northern California sheep operations in terms of coyote depredation levels, control practices, and timing of lambing (Conner 1995). Wildlife Services specialists from the U.S. Department of Agriculture conduct most coyote removal on HREC. Annual numbers of coyotes removed from HREC between 1983 and 1994 ranged from 8 to 18 (Conner 1995). Coyotes also were removed from 3 adjacent properties, including 40–45 coyotes from 1 ranch between 1982 and

1993. All removal efforts at HREC were suspended during April 1993–April 1994 to permit live-capture of coyotes for radiocollaring. Live-capture efforts continued coincident with removal efforts during April–December 1994.

METHODS

Radiotelemetry

We captured 17 coyotes between April 1993 and December 1994, using number 3 coil-spring, padded-jaw foothold traps or snares with stops to prevent strangulation. Animals were restrained without chemicals and were weighed, measured, aged, sexed, ear-tagged, radiocollared, and examined for reproductive activity and overall condition. Ages (juv: <1 yr; yearling: 1–2 yr; ad: >2 yr) of all coyotes were estimated by incisor wear (Gier 1968). Twelve radiocollared coyotes were recovered after death and aged by counting the cementum annuli of a lower canine (Matson Laboratory, Milltown, Montana, USA). Due to transmitter failure ($n = 2$) or death ($n = 1$), 3 coyotes were not monitored long enough to be used in analyses. Capture and handling procedures were approved by the University of California at Berkeley Animal Care and Use Committee (Protocol R190-0496).

We obtained locations ($n = 6,181$) of 14 radiocollared coyotes during September 1993–December 1995 by using a combination of stationary tracking units (Sep 1993–Dec 1994) and mobile, hand-held units (Jan 1995–Dec 1995). We used program LOCATE II to calculate location estimates from multiple azimuths (Pacer, Truro, Nova Scotia, Canada). Mean errors for reference radiocollars (known locations) were 230 m (95% of errors were ≤ 522 m) when we used fixed stations (usually 1–3 km from transmitters), and 146 m (95% of errors were ≤ 356 m) when we used hand-held antennas (usually 0.5–1.5 km from transmitters; Sacks 1996). We conducted radiotelemetry daily but with varying schedules. During September 1993–December 1994, tracking occurred in 2–4 blocks of 2–4 hr spread evenly over a 24-hr period. Beginning in January 1995, tracking was conducted at all hours for varying lengths of time but most intensively during 0500–0900, when we expected most sheep depredations to occur (Henne 1975).

Breeding status of females was determined by examination of mammae, association with

pups or dens, association with a radiocollared male, or postmortem examination of the reproductive tract. Resident males were assumed breeders if >40% of locations were <200 m from breeding females (or <15° for 1 pair in which the male could only be consistently received from a single fixed station; Sacks 1996). This cutoff was based on average association frequencies of 47% in mated pairs (compared to 14% between breeding females and nonbreeding male associates) as calculated from data by Andelt (1985). Coyotes were assumed nonbreeders when they exhibited transient space-use patterns (Camenzind 1978, Andelt 1985).

Territoriality

To investigate territoriality, we calculated annual home ranges for breeding coyotes monitored ≥ 9 months (no nonbreeder was monitored this long). We calculated adaptive kernel (AK; Worton 1989) 90% isopleth (home range) estimates and 65% isopleth (core) estimates via program CALHOME (Kie *et al.* 1996). The 90% AK isopleth was chosen to represent the outer boundary of the home range (territory) because its area was approximately equal to the 95% minimum convex polygon (MCP; B. N. Sacks, unpublished data) commonly used to represent coyote home ranges (e.g., Andelt 1985). The 65% isopleth was chosen to represent the core area because this proportion is analogous to 1 standard deviation from the home range center (Shivik *et al.* 1996). The periphery of an individual's home range was defined as the area between the home range and core isopleths (Windberg and Knowlton 1988).

Radiolocations of nonbreeding coyotes (residents and transients radiotracked for 2–7 months) were examined to determine whether they avoided territories of conspecifics. Breeding coyotes could not be similarly examined, because they rarely left their territories. Nonbreeder locations were often distributed among several noncontiguous areas. In cases where 1 area contained most (>50%) locations, core areas were calculated. These individuals were juveniles and yearlings, which suggested cores corresponded to natal territories (Harrison *et al.* 1991). Individuals without “cores” were considered transients. We used chi-square goodness-of-fit tests to investigate whether nonbreeding coyotes avoided other territories. Relative proportions of 3 area types contained within the

95% MCP of each nonbreeder were calculated as (1) territory periphery, (2) territory core, and (3) interstitial space (area outside 90% AK territories). Expected numbers of extra-core or transient locations in each area type were calculated from these proportions, under the null hypothesis that nonbreeders did not avoid other territories.

Determination of Sheep-Killing Coyotes

Pastures with sheep were checked from roads daily for carcasses (kills and natural deaths). During lambing periods (1 Jan–31 May), pasture searches also were conducted on foot. Searches accounted for approximately half of all dead or missing sheep (Sacks 1996). Thorough foot searches of a subset of pastures suggested causes of mortality were distributed similarly between discovered and undiscovered carcasses (Neale et al. 1998). The ratio of kills found to missing sheep also was similar across spatial units, suggesting searches were not severely biased by territory (Sacks 1996).

Field necropsies of sheep carcasses were performed to determine cause of death. Subcutaneous hemorrhaging in the throat region, canine punctures, and characteristic feeding on the rump, thighs, and shoulder were used to identify coyote kills (Wade and Bowns 1982). Tracks, hair on nearby fences, and other sign also were used to aid in determination of responsible predators. Approximate time of death of sheep killed during lambing 1995 was estimated based on body temperature relative to ambient temperature (Cox et al. 1994).

Radiotelemetry was coupled with pasture searches and necropsies to determine individuals responsible for kills. During lambing 1994, most kills were found in the territory of a radiocollared, breeding male. Because he had a weak transmitter, his signal was rarely received from >1 fixed station (all 1994 data came from fixed-station tracking). Due to the potential importance of this individual in depredation during lambing 1994, we evaluated his responsibility for sheep kills by using azimuths from the fixed station in the center of his territory that consistently received his signal (Sacks 1996). Other coyotes (with fully functioning radio-transmitters) that were radiocollared at this time played a minor role in depredations (Conner 1995, Sacks 1996).

We made a more comprehensive effort to quantify sheep-killing by individual coyotes dur-

ing lambing 1995. Confidence rankings of 1 (highly suspect) or 2 (suspect) were assigned to coyotes suspected of a kill, depending on their proximity to the kill and other evidence. Determinations were made soon after discovery of a kill, when all evidence was fresh. A rank of 1 usually indicated the individual was radiolocated at the site of the kill or in a thicket directly adjacent to a grassy area containing the kill site on the night or morning of the kill (Sacks 1996). Occasionally, a rank of 1 was assigned to an individual when the kill occurred between radio-locations made the previous evening and the morning following the kill, particularly when other evidence (e.g., scats containing wool found near the suspect) suggested the individual's presence at the kill site. Such assignments were sometimes necessary during pup-rearing season (Apr–Aug) when breeders spent little time at kill sites before returning to dens (Sacks 1996). The 2 rank was used only when information (estimate of kill time, radiotelemetry, supporting evidence) was insufficient to assign a 1. A rank of 2 only indicated that the kill was found in the territory of a resident individual or, if a transient, that the individual was closer than usual to the kill site the day before or after the kill. In some cases, >1 individual or pair was assigned a 2 for the same kill (e.g., if the kill was located where territories met, and no coyote was located at the kill). Kills were assumed to be made by uncollared coyotes when they occurred outside territories of radiocollared coyotes, and when radiotelemetry provided alibi for all radiocollared individuals.

RESULTS

Seven breeding coyotes (M302, M208, M106, F203, F102, F109, F104 [first character indicates sex]), 5 nonbreeding resident coyotes (M19, M303, M205, F101, F198), and 2 individuals that apparently changed breeding status from 1 year to the next (F210: breeder in 1994, transient nonbreeder in 1993 and 1995; M209: transient nonbreeder in 1994, breeder in 1995) were tracked for 2–26 months each (\bar{x} = 14.3 months). Mates of pairs (n = 4) were fixed together 49–78% of the time.

Territoriality

Breeding coyotes maintained mutually exclusive territories (Fig. 1), and annual 90% AK home ranges of neighboring pairs overlapped only to a maximum of 4% (proportion of terri-

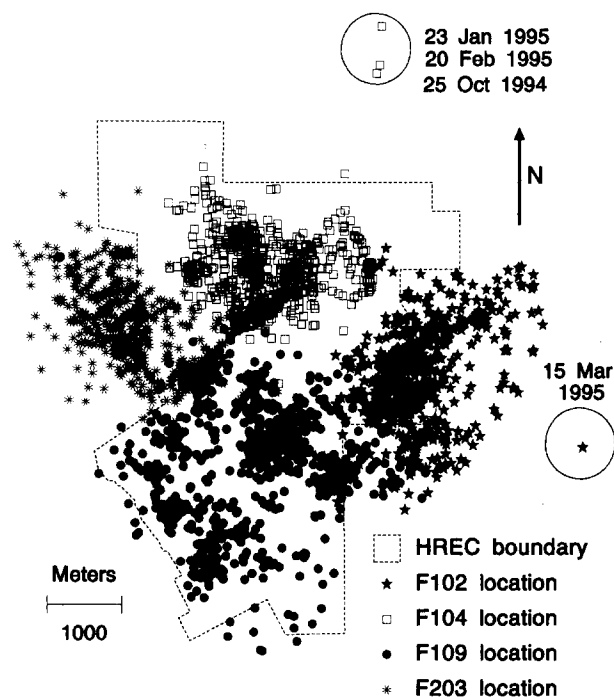


Fig. 1. Radiotelemetry locations of 4 breeding female coyotes, Hopland Research and Extension Center (HREC), June 1994–October 1995. Locations of F102 and F109 within F203's territory occurred after F203 and her mate were removed in May 1995 (Sacks 1996); F109 began to shift her home range into this territory 1 month after F203's removal. Forays of F104 and F102 are circled. Only females are shown, because males were radiocollared in only 2 of the 4 territories. Radiocollared males used the same areas as their mates.

tory overlapped by another). Annual territories were small (90% AK: $\bar{x} = 4.6 \text{ km}^2$, range = 3.0–7.4, $n = 5$; 95% MCP: $\bar{x} = 5.0 \text{ km}^2$, range = 3.2–7.9). Core areas of breeders in neighboring territories never overlapped, and breeding adults rarely took forays (usually <24 hr) from their territories (Fig. 1).

Nonbreeders generally avoided conspecific territories and spent more time than expected by chance in peripheral or interstitial space (Table 1). Nonbreeding juveniles (M19, M303, F198) and yearlings (M205, F101) associated

with territories varied in their degree of residence (Fig. 2). Two adult transients (M209: Sep 1993–Aug 1994; F210: Sep 1994–Aug 1995) were not associated with territories.

Territories of radiocollared breeders often were shared with nonbreeding pack associates. In 3 of 4 such territories, breeding adults were seen accompanied by a third uncollared adult or yearling at the den. There also was evidence of a pack associate in the fourth territory (F203's), as a nulliparous yearling female was snared and killed in the territory in denning

Table 1. Ratios of observed to expected numbers of locations of 5 nonbreeding coyotes in cores (65% adaptive kernel [AK] isopleths) and peripheries (between 65 and 90% AK isopleths) of territories of conspecifics, and in interstices among territories (outside 90% AK isopleths), Hopland Research and Extension Center, January 1994–March 1995.

Coyote ^a	Cores	Peripheries	Interstices	n^b	χ^2_2	P
F101	0.50	0.77	1.29	77	6.05	0.049
M205	0.74	0.92	1.42	64	4.52	0.104
F198	0.47	1.25	1.67	53	12.93	0.002
M209	0.58	1.43	0.31	61	12.64	0.002
F210	0.14	1.26	1.48	168	54.89	<0.001

^a Two nonbreeding individuals (M19, M303) were alive and radiocollared only in periods when no territorial individuals were radiomonitored and therefore could not be included in this analysis.

^b Number of extra-core or transient locations.

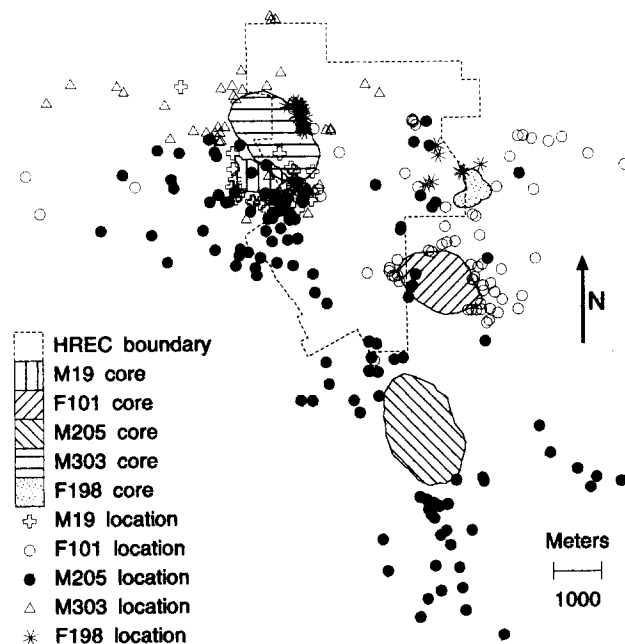


Fig. 2. Adaptive kernel cores (65% isopleth) and extra-core locations of 5 juvenile and yearling nonbreeding coyotes, illustrating varying degrees of residence, Hopland Research and Extension Center (HREC), September 1993–March 1995. M19 was never located far from his core; F101, M205, and M303 spent differing proportions of their time on forays from cores, and F198 dispersed from her core to a single location. F198's core was contained in the territory of breeding coyotes, F102 and M106, which suggests she was their offspring.

season. Paired tracks suggested she had been traveling with another coyote, which seemed unlikely for a transient. Also, a radiocollared yearling female (F101)—not pregnant or lactating when captured (in denning season)—used a territory-sized area, which suggested she was the nonbreeding associate of a breeding pair in that area. Although we were not able to account for all members of packs, evidence suggested packs typically had ≤ 2 associates (Sacks 1996).

Coyotes that Killed Sheep

Territorial breeders were responsible for most coyote-killed sheep in both years. Sixty-five sheep kills were found during lambing (1 Jan–31 May) in 1994. Of these 65 kills, 52 (80%) kills, composing 45 events (i.e., individuals or ≥ 2 sheep killed in the same place), were found in a single territory (M302). Furthermore, no 2 kill events in M302's territory occurred on the same night, suggesting that 1 individual or pair was responsible for most or all kills occurring there. Based on radiotelemetry azimuths, M302 spent a great deal of time in the northern region of his territory where most of these sheep were killed (Fig. 3). Radiotelem-

etry was conducted on nights (2200–2400) or mornings (0700–0900) of 26 kill events, and azimuths supported M302's association with 23 (88%) of these events. He was located at an azimuth of $\leq 30^\circ$ from kills on nights or mornings of 17 events, and his signal was not received during nights or mornings of 6 kill events that occurred in directions where his signal rarely could be received because of topography. In the remaining cases, either no signal was received when kills were in areas without topographic barriers ($n = 2$), or he was located $> 60^\circ$ from kills ($n = 1$).

Seven additional breeding coyotes from 5 pairs were radiocollared by June 1994 (including M302's mate, F109). All of their territories overlapped sheep pastures (Fig. 3). During late pup-rearing and after most lambs were sold (1 Jun–13 Aug), kills occurred primarily in 2 concentrations near clusters of locations corresponding to F109's–M302's den and to another pair (F210–M208) for which no den was found, which suggested these 2 pairs were responsible for most depredation during this period (Fig. 4A). M302 was shot on 13 August, after which time killing declined precipitously (Fig. 5),

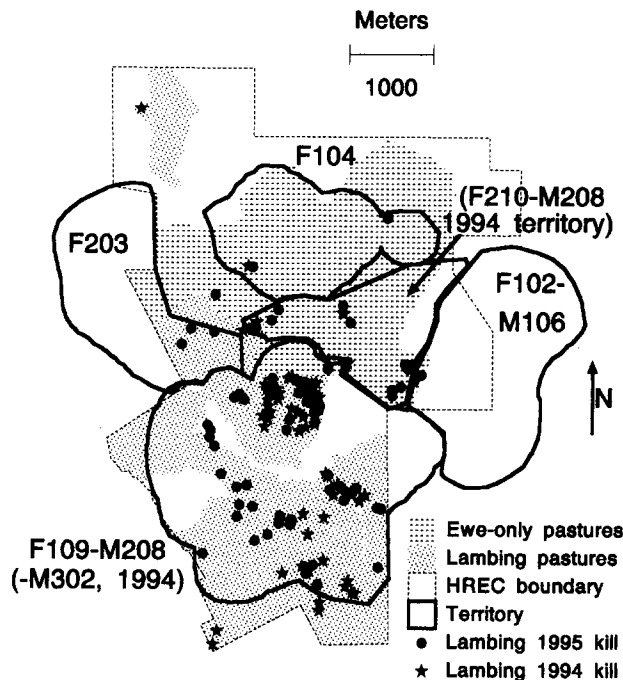


Fig. 3. Territories of radiocollared breeding coyotes in relation to sheep pasture, Hopland Research and Extension Center (HREC), June 1994–August 1995. Sheep kills are shown for lambing periods of 1994 and 1995. Territorial boundaries of radiocollared breeders were based on 90% adaptive kernel isopleths, and these were slightly modified to accommodate topographic features (e.g., streambeds, roads, deer-proof fences) likely to have served as actual territorial boundaries. The former territory of F210–M208 (Dec 1993–Aug 1994) is shown because an uncollared pair may have occupied this area concurrent with the other territories (Sacks 1996); boundaries of this territory were assumed to be common with adjacent territories.

which further supported the view that M302 was the primary killer of sheep in 1994. After his death, M302's mate, F109, paired with M208; M208's (former) mate, F210, became transient and was not subsequently associated with sheep kills. A new pair may also have moved into F210's–M208's former territory, based on sightings and vocalizations (Sacks 1996). F109–M208 continued to be associated with kills in their own territory, but neither they nor other collared coyotes were associated with kills in M208's (and F210's) former territory, which suggested uncollared coyotes (paired or not) were responsible for sheep killed there during this period (Fig. 4B).

We conducted intensive radiotelemetry during lambing 1995 to determine which individuals killed sheep. Seventy-four coyote-killed sheep were found (20 ewes, 54 lambs) during this time. Forty-four (92%) of 48 1-ranked kills were attributed to breeding adults; the other 4 were attributed to uncollared coyotes of unknown breeding status (Table 2). One pair (F109–M208) was responsible for at least 85%

of 1-ranked kills, and 55% of all kills found during lambing 1995. Because this pair was often together when sheep were killed, it was difficult to know which individual did the killing. Apparently, M208 had a unique bite pattern such that the canines rarely punctured the skin of the sheep's throat (presumably because of broken canines), but instead left large hemorrhage marks. Based on this characteristic, it appeared that he was doing most or all of the sheep-killing during the early spring, when F109 was in late gestation. Furthermore, after F109 whelped, the pair was often separated, and radiotelemetry confirmed that M208 killed most sheep during this period. After his removal, the rate of sheep killing abruptly declined (Fig. 5), as it had the previous year when M302 was removed, and the infrequent kills made by F109 showed typical canine punctures. Not only were the removals of M302 and M208 associated with declines in sheep kills, but removals of 23 other coyotes from HREC before and during the lambing period had no detectable effect on the frequency of sheep kills (Fig. 5).

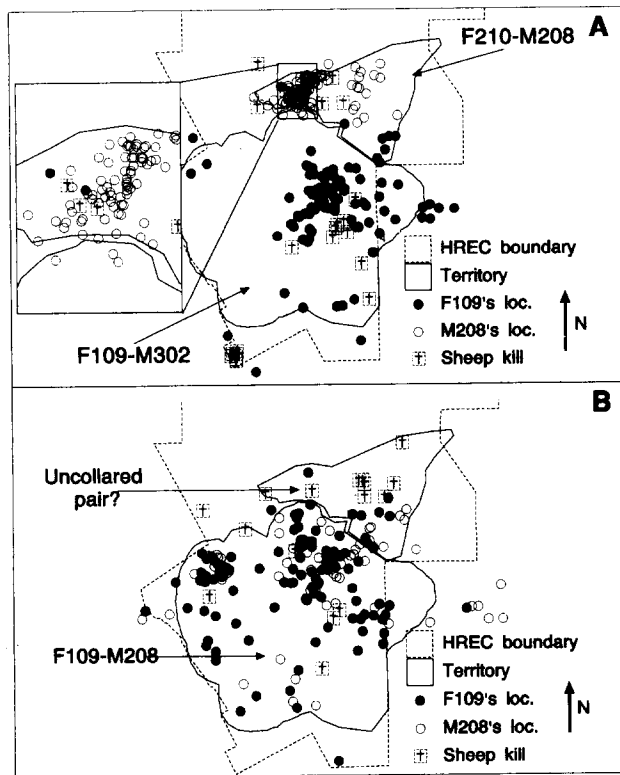


Fig. 4. Locations of F109 and M208 in relation to sheep kills during the nonlambing period in 1994, Hopland Research and Extension Center: (A) before pairing (1 Jun–13 Aug 1994), and (B) after pairing (14 Aug–30 Nov 1994). Before pairing with each other, M208 and F109 were paired with other radiocollared coyotes whose locations (not shown) were distributed similarly to their own. F109's locations were clustered around a known den during the earlier period (A). No den was found for F210, although we could not confirm that she did not have a den.

DISCUSSION

Territoriality

Breeding coyote pairs, sometimes with associates, occupy and actively defend mutually exclusive territories in widely varying environments (Camenzind 1978, Bowen 1982, Messier and Barrette 1982, Andelt 1985). Territories at HREC were mutually exclusive and were generally avoided by conspecifics. Also, 2 transient coyotes usually were most active during daytime, when residents were least active, suggesting transients avoided territorial coyotes temporally as well as spatially (Sacks 1996). Two chases of transients from territories by resident breeders were inferred from sequential radio-telemetry locations, further supporting territory defense (Sacks 1996).

Territories are not impervious to incursion by external coyotes. Coyotes were observed to scavenge ungulate carcasses in conspecifics' territories when food was relatively scarce in win-

ter (Camenzind 1978, Bekoff and Wells 1980, Bowen 1981). At HREC, wild prey (e.g., rodents, lagomorphs, blacktail deer [*Odocoileus hemionus*]) were abundant throughout the year (Neale 1996), which possibly alleviated pressure on coyotes to risk confrontation by foraging in actively defended areas. Nevertheless, some scavenging by transients on sheep carcasses probably occurred inside territory boundaries. In 1994, 2 transient coyotes were located on the periphery of a territory in the vicinity of several sheep kills around the time of the kills during lambing (Conner 1995). Kills only occurred in that area on nights when the resident breeding male (M302) was nearby, and often when transients were not (Sacks 1996). Furthermore, transients sometimes were located near kill sites the following day, suggesting they scavenged these carcasses (Sacks 1996). Similarly, Crabtree (1989) found that when transient coyotes were located in core areas of territories, they

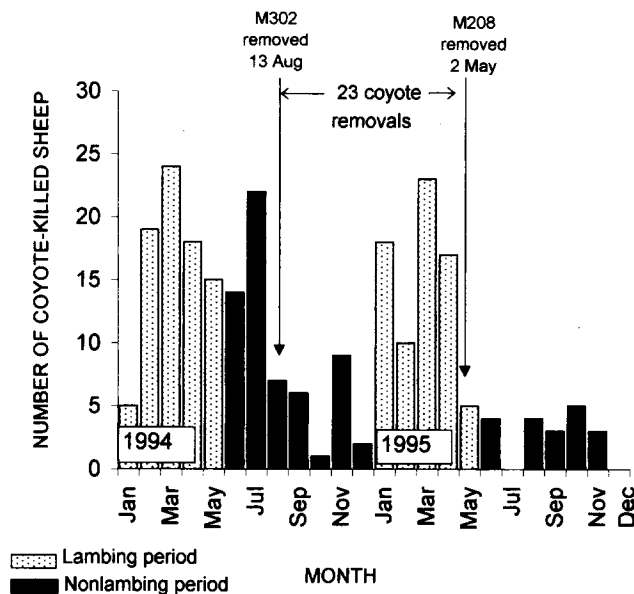


Fig. 5. Numbers of coyote-killed sheep on Hopland Research and Extension Center during lambing (mostly lambs) and non-lambing (mostly ewes) periods, January 1994–December 1995. When the 2 breeding male coyotes (M302, M208) most frequently associated (by radiotelemetry) with kills were removed, killing declined precipitously.

were often scavenging ungulate carcasses. The degree to which breeders exclude conspecifics from hunting (but not scavenging) within territories is relevant to managing sheep depredation. Coyotes probably can smell carrion from great distances, which enables them to find and consume this food in relatively brief periods of time. In contrast, hunting requires more time and energy and thus likely entails greater risk of confrontation. Therefore, hunting by tran-

sients is probably less common than scavenging in areas defended by conspecifics.

Coyotes that Killed Sheep

Our results indicate that, in any given year, most coyotes at HREC did not kill sheep. Breeding pairs whose territories overlapped sheep (especially lambs) were the principal predators of sheep. Annual numbers of sheep killed by coyotes at HREC during 1994 ($n = 134$) and 1995 ($n = 86$) were high relative to previous years ($\bar{x} = 69$, range = 21–143, $n = 22$ yr; Sacks 1996), and only a few coyotes were responsible. Based on the density of coyotes on HREC in 1995 (0.48–0.68/km²; Sacks 1996), 16% is a conservative (high) estimate of the population segment responsible for greater than two-thirds of sheep kills. The true percentage was probably smaller, because the number of individuals with home ranges partly overlapping HREC was larger than the number on HREC at any point in time.

The removal of several coyotes during the study supported our conclusions. Throughout fall and winter 1994–95, many nonbreeding coyotes were removed from HREC with no apparent effect on the numbers of sheep killed. Killing did not decline in an area until 1 member of the breeding pair (the male in both cases)

Table 2. Numbers of sheep kills attributable to radiocollared coyotes or pairs, Hopland Research and Extension Center, January–May 1995. Kills were assigned to individuals as highly suspect or suspect, depending on evidence of their involvement.

Coyote(s)	Minimum number killed (highly suspect)	Maximum number killed ^{a,b} (highly suspect + suspect)
F109–M208	41	54
F203–uncollared male	2	4
F102–M106	1	5
F104–uncollared male	0	2
F210	0	1
F198	0	0
Other uncollared coyotes	4	30

^a Maximum number of sheep kills found for which the individual or pair may have been responsible.

^b In total, 74 confirmed coyote-killed sheep were found. The maximum number of kills sum to greater than 74 because >1 individual or pair were suspects for several kills.

identified as a sheep killer was removed. These results were consistent with previous findings that depredation was only slightly negatively correlated with prior coyote removals during 13 years at HREC (Conner *et al.* 1998). In addition, breeders continued to be implicated in sheep kills beyond the termination of this study (K. M. Blejwas, University of California at Berkeley, unpublished data).

Other studies support our finding that breeding coyotes were the principal sheep predators. A study of captive coyotes at HREC determined that adult males, and females when paired with them, killed sheep more often than did yearlings and single females (Connolly *et al.* 1976). In Wyoming, sheep depredation by coyotes within approximately 1 territory width of dens usually ceased when breeding adults were removed, which suggested these individuals were responsible for most depredations (Till and Knowlton 1983). Breeding-age adult coyotes also have been disproportionately implicated in predation of other livestock, namely domestic turkeys (Althoff and Gipson 1981) and calves (Gilliland 1995). Lastly, breeding adults, compared to nonbreeders, appeared to be the most significant predators of wild ungulates as well (Harrison and Harrison 1984, Gese and Grothe 1995).

Contrary to our findings, Windberg *et al.* (1997) concluded that both resident (breeding, nonbreeding) and transient (nonbreeding) coyotes killed domestic goats because both fed on carcasses. However, because these authors did not track coyotes at kills, transients possibly scavenged goats after they were killed by resident breeding coyotes. Young and transient coyotes are known to commonly scavenge livestock kills made by other individuals (Danner and Smith 1980, Roy and Dorrance 1985, Sacks 1996).

Sheep depredation may occur principally as a consequence of provisioning pups by breeding coyotes (Till and Knowlton 1983), because it may be more efficient for coyotes that are provisioning pups to kill larger prey (Harrison and Harrison 1984). In most of the United States, lambing coincides with coyote pup rearing. However, at HREC and elsewhere in northern California, lambing occurs during winter months (Scrivner *et al.* 1985, Conner 1995), out of phase with pup rearing. Despite such timing, lamb availability alone was sufficient to explain most of the seasonal trend in lamb and sheep

depredation at HREC over 13 years, indicating that provisioning pups was not a direct cause of most sheep depredation (Sacks 1996). Provisioning pups (or other energetically costly aspects of reproduction; e.g., gestation) may provide the initial impetus for breeders to kill sheep, after which time the behavior continues habitually.

The pair bond itself may explain why breeders are more likely than nonbreeders to kill sheep and wild ungulates. Breeders tend not to be alone as often as nonbreeders (Andelt 1985, Sacks 1996), and pairs may be better able than individuals to bring down larger animals. The breeding male and female responsible for most sheep kills in 1995 of this study were usually together when killing sheep. Furthermore, Gese *et al.* (1988) found that coyotes in groups consumed more ungulate prey than did lone coyotes, and several direct observations of coyotes killing ungulates suggested coyotes hunt these prey cooperatively (Connolly *et al.* 1976, MacConnell-Yount and Smith 1978, Hamlin and Schweitzer 1979, Gese and Grothe 1995).

Although coyotes that killed the most sheep at HREC were breeders, not all breeders killed sheep. No kills were confidently assigned to a pair (F104 and mate) in a territory that overlapped ewes but not lambs (Fig. 3). However, pairs that killed lambs regularly also killed adult ewes when lambs were not present. A coyote's willingness to kill novel prey may be influenced by the size of the prey: perhaps coyotes kill lambs initially and then, as lambs grow larger, continue to prey on them into adulthood. Also, preference for sheep may increase with continuing exposure to this food source, such that longer-established residents kill sheep more frequently than do newer residents. Alternatively, preference for sheep simply may differ among breeding individuals (Till and Knowlton 1983); if so, this variability argues strongly for selective removal of problem individuals versus broadcast lethal control. The residency of a pair that did not kill sheep in an area where sheep were pastured would be expected to reduce depredation if the pair's presence kept other coyotes from killing sheep in their territory. Clearly, more information is needed to determine the variability among breeders in their propensity to kill sheep and to understand the ontogeny of this behavior in individuals.

Importance of Breeding Status

Previous radiotelemetry studies have distinguished classes of coyotes by space use (Windberg and Knowlton 1988, Gese et al. 1989, Windberg et al. 1997). This classification may obscure functional differences related to the social structure of the species if breeding status is not ascertained. The breeding pair is the fundamental social unit maintaining the territory, and the territory itself is probably best viewed as a reproductive entity (Messier and Barrette 1982). Within territories, coyotes often form packs like those of gray wolves (*Canis lupus*), typically with a single breeding pair and ≥ 1 nonbreeding associates (usually offspring; Camenzind 1978, Bekoff and Wells 1980, Andelt 1985). In addition, transient individuals normally compose 12–35% of the population at any time (Camenzind 1978, Andelt 1985, Windberg and Knowlton 1988). The distinction between resident coyotes (namely territorial breeders and nonbreeding associates) and transient coyotes has been considered more important than that between breeding and nonbreeding individuals (Windberg and Knowlton 1988, Gese et al. 1989, Windberg et al. 1997). Recent evidence, however, suggests that breeding status is primary (Gese and Grothe 1995, Hatier 1995; Gese et al. 1996a,b; this study), and that the distinction between nonbreeding pack associates and transients may be less clear and perhaps less important. Nonbreeders showed varying degrees of affiliation with territories in this study, in Quebec (Messier and Barrette 1982), and in Yellowstone National Park (Hatier 1995). Nonbreeding coyotes seem to fall on a space-use continuum ranging from completely intraterritorial to completely extraterritorial, and this pattern can change over time. Extraterritorial space use is probably associated with finding mates and breeding territories—a need unique to nonbreeders. Thus, breeders and nonbreeders represent qualitatively distinct classes of individuals, whereas “residents” and “transients” do not.

MANAGEMENT IMPLICATIONS

The primary predators of sheep were breeding adult coyotes, whose territories overlapped sheep. Furthermore, territoriality effectively precluded sheep depredation by “trespassing” coyotes. These findings suggest depredation management strategies will be successful only

insofar as they target breeding individuals. Furthermore, removal of breeders from territories overlapping sheep, but where predation is not a problem, may be counterproductive by allowing access to sheep by potential sheep-killing coyotes. In practice, removal of specific depredating individuals is difficult, and the effects of such removals are likely to be temporary. Concentrating control efforts closer to kill sites (e.g., within a territory width) could decrease removals of nonoffending individuals but would not guarantee removal of target coyotes. Future research should evaluate removal techniques with respect to their specificity to breeding adults and efficacy in relation to the phenology of lambing and coyote reproduction. Our conclusions are consistent with what is known about coyote sociality in other areas. Thus, the results of this study likely are applicable where coyotes and sheep co-occur. However, wild prey abundance may influence the degree to which coyote sociality influences predation patterns. Future studies on the role of sheep in the overall foraging ecology of coyotes will further elucidate the ecological context of depredation.

ACKNOWLEDGMENTS

We are indebted to K. M. Blejwas, J. P. Dayton, J. A. Meisler, J. Poor, Jr., and T. J. Weller for their many long hours spent tracking and trapping coyotes. S. A. Ardley, J. Theade, E. Voight, and University Research Expedition Program volunteers also provided assistance in the field. We thank F. F. Knowlton, E. M. Gese, P. S. Gipson, M. W. Fall, S. P. Riley, and the Steve's Pizza reading group at the University of California, Davis, for insightful comments on earlier drafts of this manuscript. Conversations with K. M. Blejwas, E. M. Gese, and G. Johnson were also helpful. We also thank R. M. Timm for use of facilities at HREC, and J. W. Marston and M. M. Conner who helped in various ways. This study was funded primarily by the U.S. Department of Agriculture's National Wildlife Research Center through cooperative agreements with the University of California at Berkeley (12-34-74-0235-CA) and with the University of California Division of Agriculture and Natural Resources (12-34-74-0224-CA). Additional support was provided by the University of California at Berkeley through the Wildlife Graduate Student Fund of the Department of Environmental Science, Policy, and Management.

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Received 28 March 1998.

Accepted 28 August 1998.

Associate Editor: Hellgren.